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THE UNIVERSITY OF ALBERTA

QUANTITATIVE GENETICS OF SUBSTITUTION LINES INVOLVING CHROMOSOME I OF COMMON WHEAT

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF PLANT SCIENCE

by
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ABSTRACT

An analysis of the genetics of the quantitative characters height, number of days to heading, weight per plant, and number of tillers per plant was made using a method based on monosomic breeding procedures.

It was found that one gene with pleiotropic effects was responsible for most of the genetic differences among the substitution lines. The gene is not on chromosome I. It was also found that four genes may differentiate Thatcher from Chinese Spring wheat with respect to earliness. The same four genes may be responsible for most of the genetic variation for yield observed in the backcross progeny resulting from a cross between Chinese and Thatcher.

An appraisal of the monosomic procedure for the genetic analysis of quantitative characters is made.

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INTRODUCTION

Most of the variation in populations of plants and animals is quantitative.

In recent years it has become evident that for a satisfactory elucidation of quantitative genetic phenomena, experimental techniques must be devised to provide solutions to problems concerning:

(1) the number and magnitude of effects of genes influencing quantitative characters,

(2) the importance and the nature of the pleiotropic effects of individual genes, and in general,

(3) the action and interaction of the individual genes responsible for the genetic component of quantitative variation.

Two genetically pure varieties of a species might be expected to differ by many genes which affect quantitative characters in such a way that Mendelian techniques of genetic analysis cannot be used (see Mather, 1949). However, it is conceivable that each chromosome of the two varieties might differ by relatively few genes.

Unrau (1958) has suggested a method for determining the number and the recombination relationships of genes on a specific wheat chromosome which affect quantitative characters. This paper deals with an experimental study of the genetics of some quantitative traits in several chromosome I substitution lines in common wheat (*Triticum aestivum* Lin.) using the technique outlined by Unrau.

LITERATURE REVIEW

A. The Genetics of Quantitative Characters

For reasons of brevity only the literature that is most relevant to the results of this investigation is reviewed.

It is generally assumed by biometrical geneticists that many genes with small and similar effects are involved in the inheritance of quantitative characters. Mather (1949) states, "The fine gradation in the manifestation of a character showing continuous variation suggests that the number of genes, whose differences control the variation is large; certainly of the order of 10^1 and possibly of the order of 10^2."

In the same publication Mather also states, "In order to account for continuous variation we have to postulate systems of genes having small, similar and supplementary effects." Falconer (1960) states, "The genetic variation of metric characters appears from the results of experimental selection to be the product of segregation at some hundreds of loci, or more probably some thousands if the variation of all characters is included."

However, several investigators have found examples of relatively simple inheritance of certain quantitative characters. Among recent reports of simple inheritance of quantitative characters are the following: Frey (1954) found that two genes were involved in the inheritance of heading date in barley. Allard (1956a) found that three major genetic units were transmitted as entities in the inheritance

of seed size in lima beans. Allard (1956b) found that at least three-fourths of the genetic variability in heading date in a cross between the wheat strains 3859 and Baart 46 was due to a single gene. Johnson and Paul (1958) found that two main genes were involved in the inheritance of earliness in barley. Leonard, Mann and Powers (1957) found that two genes conditioned plant height in barley (Baitori No. 10 x Club Mariout).

That the determination of the number of genes involved in quantitative inheritance is of practical as well as academic interest is stressed by Mather (1960) who states, "Without reliable estimation of the number of effective factors the balance between potential and free variability cannot be struck and the magnitude of ultimate response to selection cannot be calculated. The derivation of reliable methods of estimation is long overdue."

Another problem of considerable importance is the nature of the correlated responses to selection often observed in experiments. Falconer (1960) states, "The genetic cause of correlation is chiefly pleiotropy, though linkage is a cause of transient correlation particularly in populations derived from crosses between divergent strains." Mather (1949) states, "Genetical experiments have in fact shown that genes of unlike effect are characteristically mingled along the chromosomes. Apparent pleiotropic action, due really to linked genes, must therefore be expected, and the observations on correlated responses to selection vindicate this expectation .... Pleiotropy in the classical sense is therefore almost useless as a concept for application in biometrical genetics. We know that apparent pleiotropy

can be due to linkage and we know that units of inheritance are linked groups of genes. We have, and indeed we can have, no proven case of pleiotropy of a single polygene." Similar views are expressed in a publication by Breese and Mather (1960).

B. The Genetic Analysis of Quantitative Characters in Wheat using Whole Chromosome Substitution Lines

Kuspira and Unrau (1957) used the Thatcher, Hope and Timstein sets of substitution lines in Chinese Spring wheat, which were produced by Sears *et al*. (1957), in an investigation designed to determine the effect of individual chromosome substitutions on the quantitative characters height, days to head, lodging resistance, protein content, 1000 kernel weight, spike density, and yield. It was found that a number of the substitution lines differed significantly from Chinese Spring wheat in each of the characters studied. In particular, it was found that the substitution line which had chromosome I of Thatcher substituted for its homologue in Chinese Spring wheat was significantly earlier, more lodging resistant, higher yielding, and had a higher 1000 kernel weight and a less dense spike than Chinese Spring wheat.

MATERIALS AND METHODS

Description of Substitution Lines

The three substitution lines used in this study are basically lines of Chinese Spring wheat (Triticum aestivum L.) in which chromosome I of Chinese has in each case been replaced by chromosome I of the "donor" varieties Thatcher, Timstein and Hope. The three substitution lines will henceforth be referred to as C.S. (2 I That.), C.S. (2 I Tim.) and C.S. (2 I Hope) respectively, and the variety Chinese Spring will be referred to as Chinese or C.S. The method of producing substitution lines has been outlined by Sears (1953).

According to Kuspira (Personal Communication) a total of 5 backcrosses were made to Chinese monosomic I in the production of the chromosome I substitution lines used. The probability (P) that a particular gene on a "background" chromosome (i.e., a chromosome other than chromosome I) of a "donor" variety will be incorporated in a substitution line is $P = (1/2)^5 = 1/32$. Assuming that the genes by which Chinese and a "donor" variety differ are randomly distributed among the 21 pairs of chromosomes of wheat, then the probability that a particular gene is on chromosome I is $P = 1/21$. The probability that a particular gene from a "donor" variety is present in a given substitution line is equal to the probability that the gene is on the substituted chromosome plus the probability that the gene is on a "background chromosome" and is retained throughout the backcross program, that is $P = 1/21 + 20/21 \times 1/32$. The probability that any single gene difference between a substitution line and Chinese is due to a

gene on a "background chromosome" is then

$$P = (20/21 \times 1/32) \; / \; (1/21 + 20/21 \times 1/32) = 20/52.$$

Since this is not a negligible probability it is essential that the experimental procedure be designed in such a manner that it is possible to determine whether a gene is or is not on chromosome I.

If a gene, say A, on a "background chromosome" is transferred from a donor variety to a substitution line it will, of course, initially be in the heterozygous, say Aa, condition. In subsequent generations, and in particular during seed multiplication, plants with genotypes AA, Aa and aa will be produced. If the allele A confers great selective advantage on plants carrying it, as for example a gene conferring earliness would in a northern area, then in a few generations most of the plants in the substitution line should be of genotype AA.

The Experimental Procedure

For illustration purposes the fate of a hypothetical gene A, present as the AA genotype on a "background chromosome", and the fate of two genes B and C on chromosome I of a substitution line, will be considered in a cross between a substitution line and Chinese where Chinese has the genotype $\frac{a}{a}\;\frac{bc}{bc}$.

The experimental procedure used in this investigation consisted of the following steps:

(1) The substitution lines and the variety Chinese were intercrossed to produce the six F_1 hybrids: C.S. x C.S. (2 I That.),

C.S. x C.S. (2 I Tim.), C.S. x C.S. (2 I Hope), C.S. (2 I Tim.) x C.S. (2 I That.), C.S. (2 I Tim.) x C.S. (2 I Hope) and C.S. (2 I Hope) x C.S. (2 I That.).

The hypothetical genotype of F_1 plants will be $\frac{A}{a}$ for the gene on a "background chromosome" and $\frac{BC}{bc}$ for the genes on chromosome I.

(2) The six F_1 hybrids used as males were crossed with Chinese monosomic I plants.

The plants produced from the resulting seed should segregate in a 1Aa : 1aa genotypic ratio for the hypothetical gene on a "background chromosome". About 25% of the plants should be disomic and 75% should be monosomic (see Sears, 1953). The monosomic plants should have only one chromosome I rather than a pair and that should be a recombinant or non-recombinant chromosome derived from the F_1 hybrid parent. The monosomic plants should therefore segregate in a genotypic ratio of

$$\frac{(1-p)}{2}\,\frac{BC}{o} : \frac{(1-p)}{2}\,\frac{bc}{o} : \frac{p}{2}\,\frac{Bc}{o} : \frac{p}{2}\,\frac{bC}{o}$$

where p is the recombination fraction between the two hypothetical genes on chromosome I.

(3) The monosomic plants in each of the six resulting backcross families were selected on the basis of root tip cytological analysis. The monosomic plants (hereafter referred to as B_1 plants) were then selfed and permitted to produce seed.

Each B_1 plant of genotype Aa should on selfing give rise to plants of AA, Aa and aa genotypes in a ratio of 1 : 2 : 1, and each B_1 plant of genotype aa should give rise only to plants of aa genotype.

The over-all genotypic ratio expected in the progeny of B_1 plants is then 1AA : 2Aa : 5aa. Because each B_1 plant carries only one recombinant or non-recombinant chromosome I, all of its monosomic offspring should carry a genetically identical chromosome I and all of its disomic offspring should carry two genetically identical chromosome I's derived from it.

(4) Root tips from the progeny of each B_1 plant were analyzed cytologically. Whenever possible two disomic plants were selected from the progeny of each B_1 plant, otherwise one disomic or one or two monosomic plants were selected from each progeny. Hereafter the selected plants will be referred to as B_{10} plants. A total of 395 B_{10} plants were selected.

The inclusion of two B_{10} plants from each B_1 parent plant whenever possible makes possible a test of whether or not a particular gene is on chromosome I, because if and only if the gene is on chromosome I both B_{10} plants always carry the same allele of the gene.

(5) The seed obtained from each B_{10} plant was sown separately. The lines so obtained are designated B_{100} lines. The B_{100} lines were included in replicated field trials. In every case the design used was a simple lattice with single row plots spaced one foot apart. Each plot was seeded with ten seeds spaced five inches apart within the row. In the case of the families C.S. x C.S. (2 I Tim.), C.S. x C.S. (2 I Hope), C.S. (2 I Tim.) x C.S. (2 I Hope), and C.S. (2 I Hope) x C.S. (2 I That.), all of the B_{100} lines in each family were included within the same experimental design. The disomic B_{100} lines and the monosomic B_{100}

lines of each of the families C.S. x C.S. (2 I That.) and C.S. (2 I Tim.) x C.S. (2 I That.) were included in separate experimental designs.

The plots were seeded on June 9 - 10, 1960, and harvested on September 16 - 17, 1960.

Methods of Collecting Data

Each plant of each row was recorded as headed when three-fourths of the first head appeared above the flag leaf. The median number of days to heading was considered to be representative of each row and was used in the statistical analysis.

Shortly before harvest the median height in inches of the individual plants in each row was measured in the field and recorded.

Shortly after harvest the number of tillers per row and the number of plants per row were counted and recorded.

The harvested wheat was dried until a constant weight was reached. The wheat from each plot was then threshed and the total weight of plants and the total grain weight were recorded.

Methods of Analysis

The recorded field data were analyzed by the standard method for simple lattice analysis outlined in Cochran and Cox (1957). Whenever missing plots occurred, the missing plot estimation formula on page 413 of Cochran and Cox (1957) was used. All statistical analyses were done by digital computer.

Whenever a significant F value for the segregation of a character was obtained, the distribution of the B_{100} line means for the character was plotted on graph paper and an attempt was made to determine whether the distribution was into distinct classes. When no distinct classes were evident, a biometrical analysis of the data was attempted.

EXPERIMENTAL RESULTS

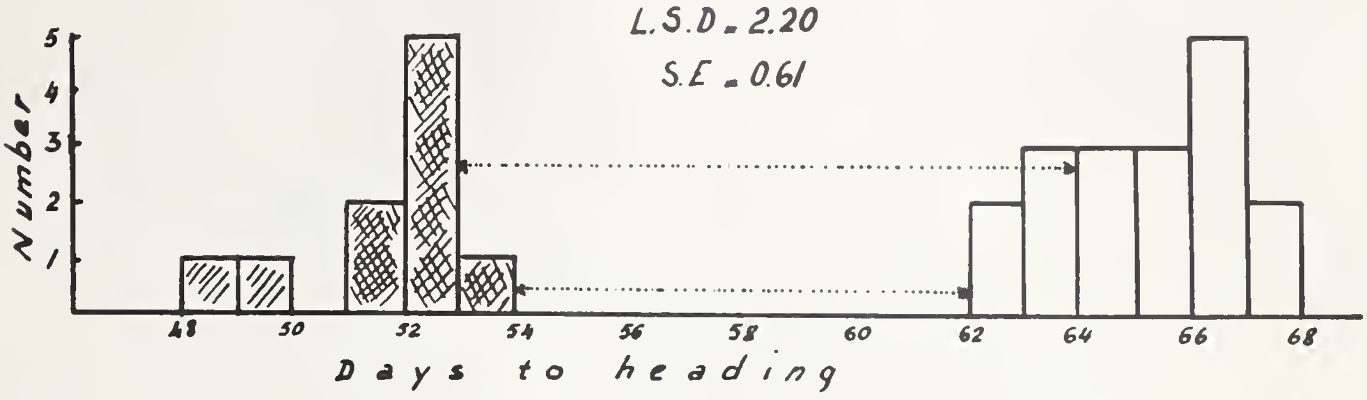
The Inheritance of Earliness

The B_{100} lines from both disomic and monosomic B_{10} parents in each of the families C.S. x C.S. (2 I That.), C.S. (2 I Tim.) x C.S. (2 I That.) and C.S. (2 I Hope) x C.S. (2 I That.) appeared to segregate into two distinct groups when the lines were classified for the character number of days to heading. The frequency distributions for number of days to heading of the B_{100} lines of the families mentioned above is shown in Figures 1 and 2.

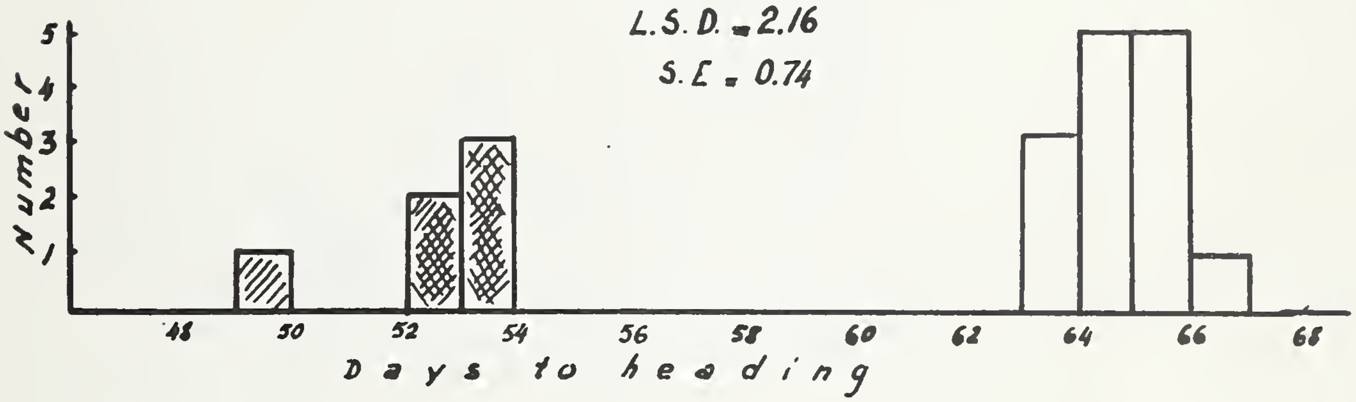
It was found that in a number of cases B_{100} lines from the same B_1 parent fell into different classes. (Such occurrences are indicated by the dotted lines in Figures 1 and 2.) This indicates clearly that the gene or genes responsible for the segregation of the character number of days to heading into two main classes is not on chromosome I.

If it is assumed that one gene is responsible for the observed segregation into two groups and that the dominant allele (designated E) of the gene is found in the homozygous condition on a "background chromosome" of C.S. (2 I That.), the expected genotypic ratio of B_{10} plants is 1EE : 2Ee : 5ee. Therefore, in the early group one third of the B_{100} lines should contain only early plants of EE genotype and two thirds of the B_{100} lines should segregate in a 3 : 1 ratio for early (EE and Ee) and late (ee) plants.

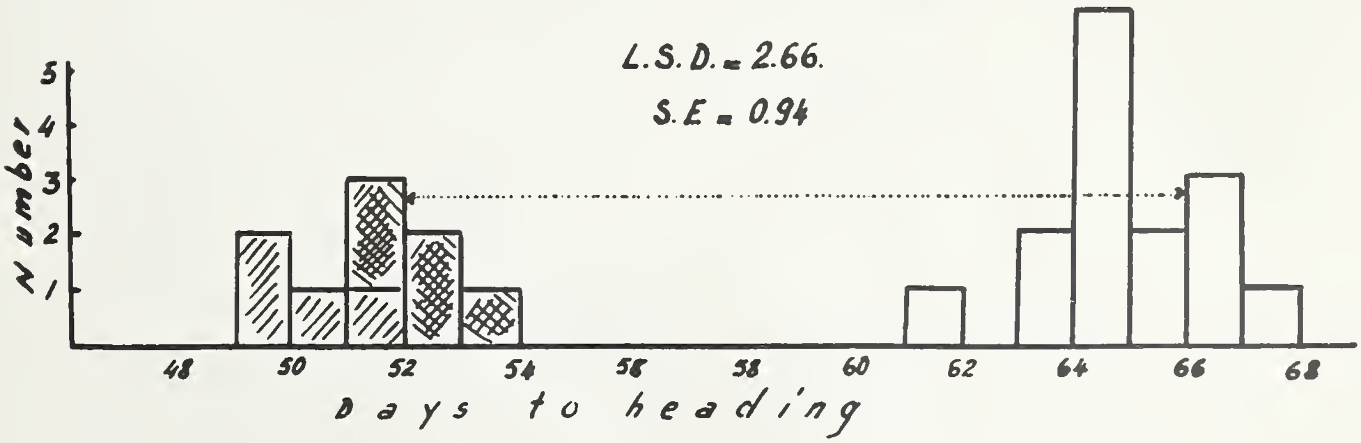
C.S. x C.S. (2 I That.) Disomic B_{100} Lines



C.S. (2 I Tim.) x C.S. (2 I That.) Disomic B_{100} Lines



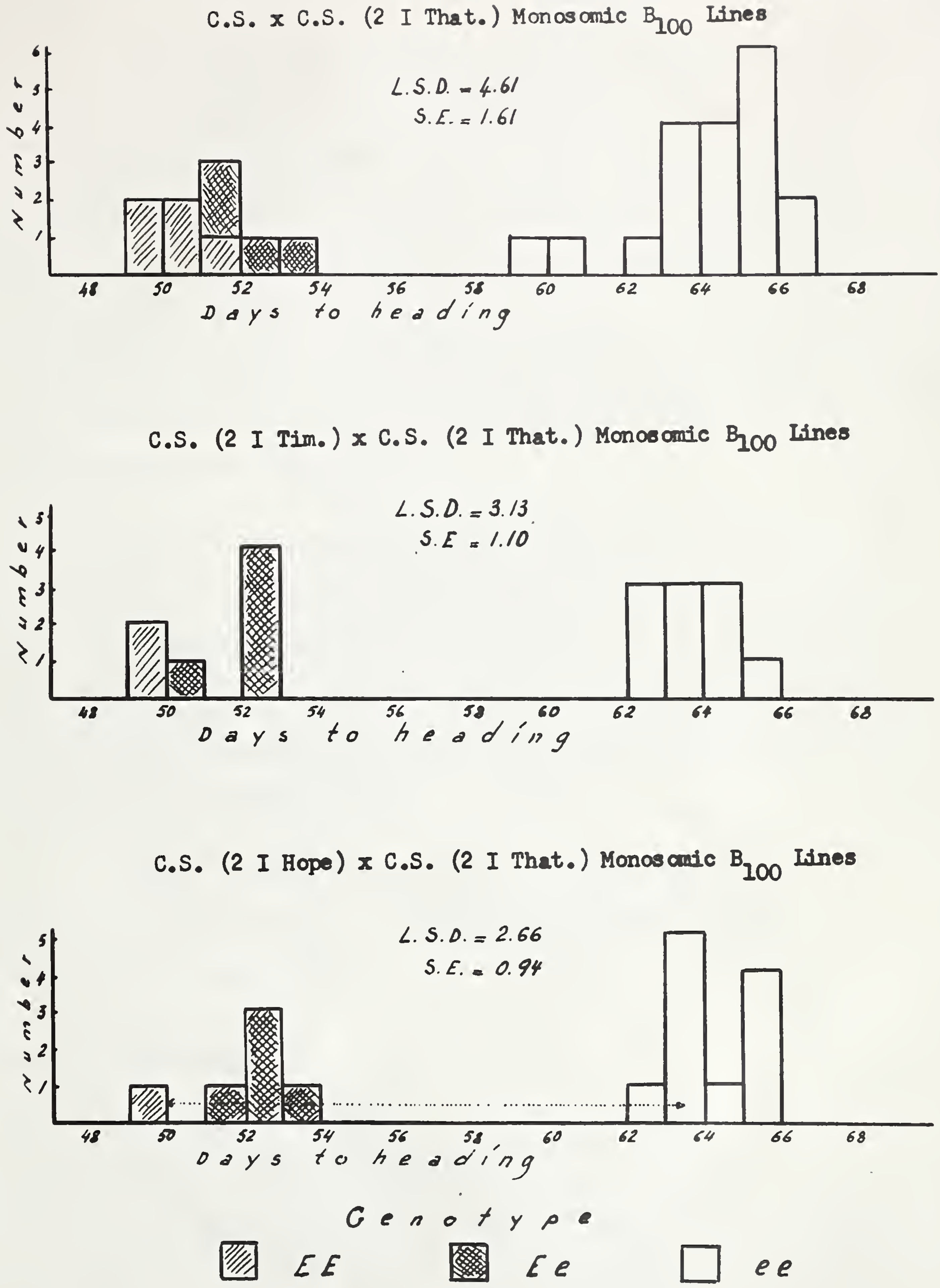
C.S. (2 I Hope) x C.S. (2 I That.) Disomic B_{100} Lines



Genotype

▨ EE ▩ Ee ☐ ee

Figure 1. Frequency distribution for days to heading



C.S. x C.S. (2 I That.) Monosomic B_{100} Lines

C.S. (2 I Tim.) x C.S. (2 I That.) Monosomic B_{100} Lines

C.S. (2 I Hope) x C.S. (2 I That.) Monosomic B_{100} Lines

Figure 2. Frequency distribution for days to heading

On the basis of the presence or absence of segregation for earliness within each early B_{100} line, the genotype of its B_{10} parent was assigned and is indicated in Figures 1 and 2. It was found that the ratio of EE, Ee and ee B_{10} plants was 15 : 32 : 87. The X^2 for goodness of fit of the observed ratio to that expected on the hypothesis of a 1 : 2 : 5 ratio is

$$X^2 = (15-16.75)^2 / 16.75 + (32-33.5)^2 / 33.5 + (87-83.75)^2 / 83.75 = 0.378$$

with $0.95 > P > 0.50$. This fit is obviously a good one and indicates that the hypothesis holds.

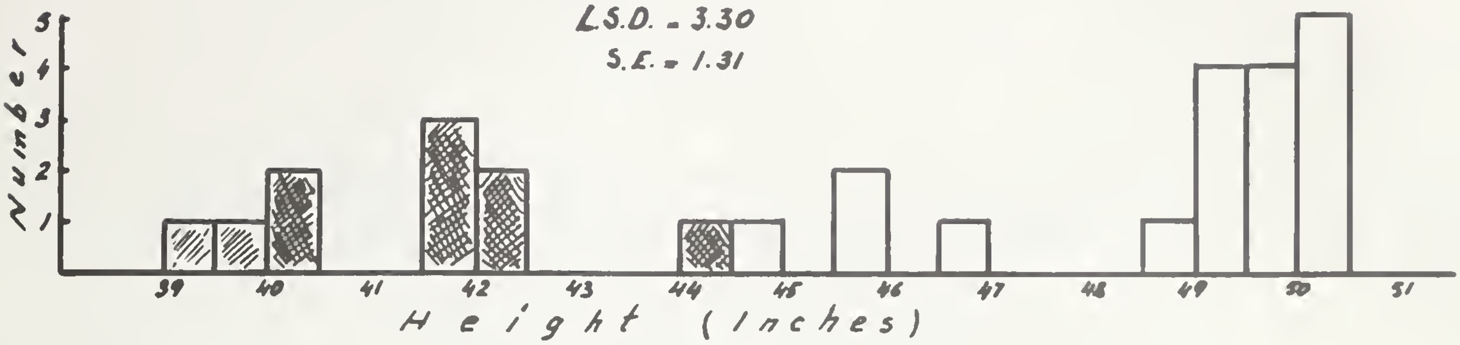
It may be of interest to note that the source of the seed which gave rise to ee plants seemed to have a marked effect on heading date, and in fact ee parental lines grown from seed harvested in the field in the fall of 1959 headed in approximately seven fewer days than ee lines grown from seed harvested in the greenhouse in the late fall of 1959 or in the spring of 1960.

The possibility that genes with very minor effects on earliness segregated in any of the six families studied will be considered in a later section.

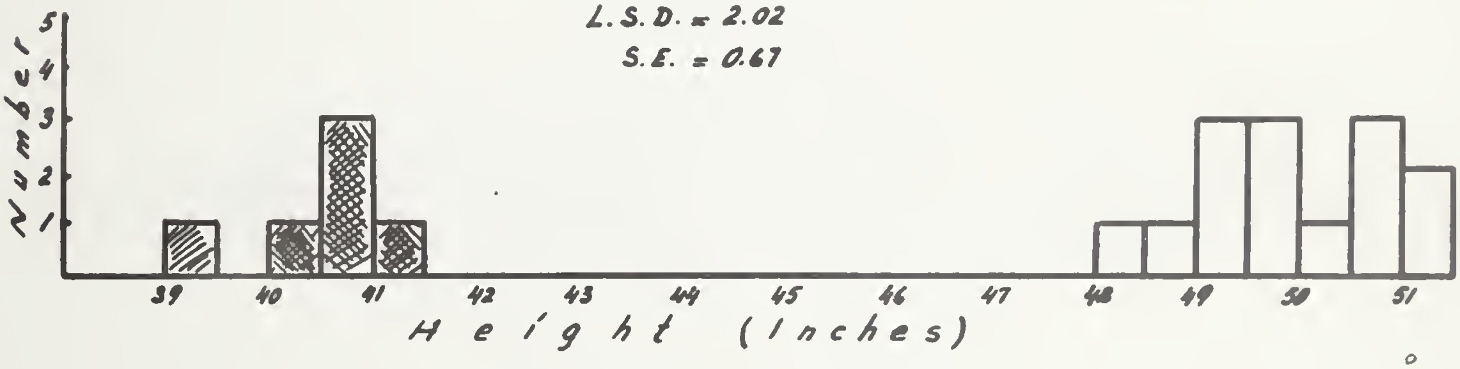
The Inheritance of Height

The frequency distributions for height in inches of the B_{100} lines in each of the families C.S. x C.S. (2 I That.), C.S. (2 I Tim.) x C.S. (2 I That.) and C.S. (2 I Hope) x C.S. (2 I That.) is presented in Figures 3 and 4. Separate distributions are presented for the B_{100} lines derived from monosomic B_{10} parents and for those derived from disomic B_{10} parents.

C.S. x C.S. (2 I That.) Disomic B_{100} Lines



C.S. (2 I Tim.) x C.S. (2 I That.) Disomic B_{100} Lines



C.S. (2 I Hope) x C.S. (2 I That.) Disomic B_{100} Lines

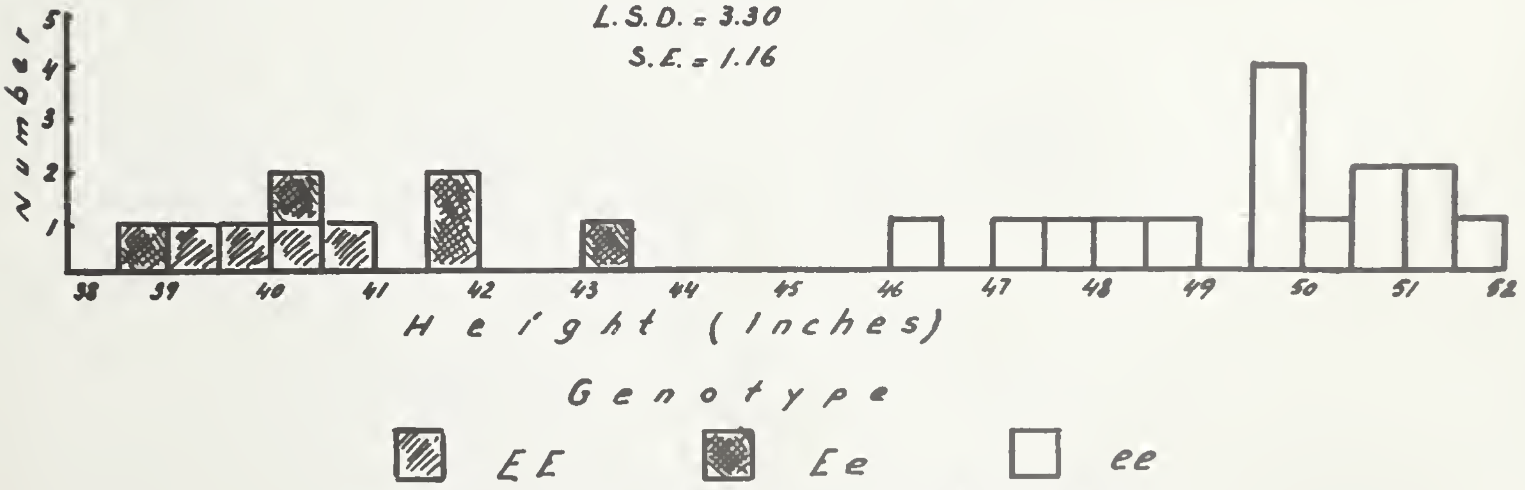
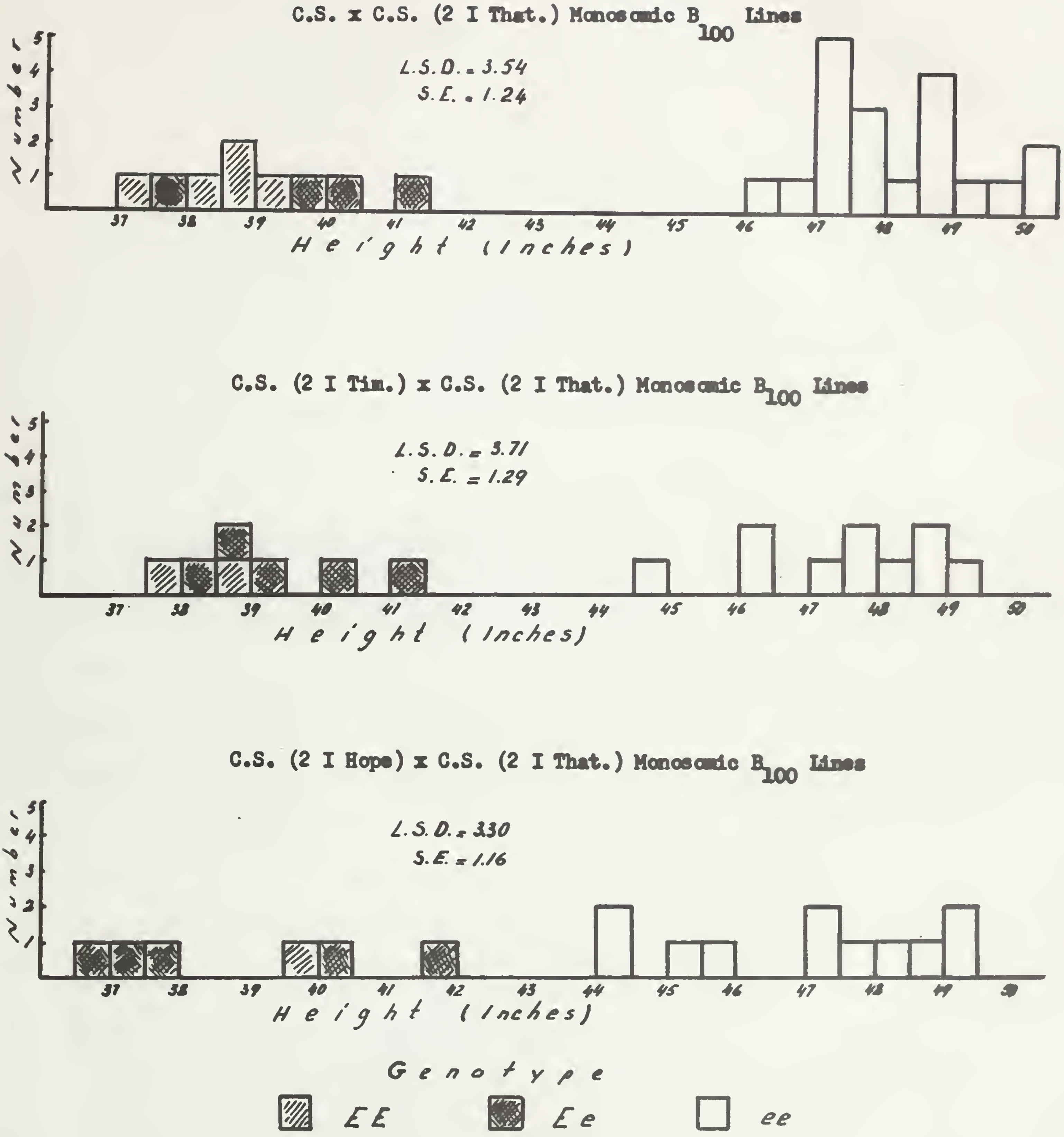


Figure 3. Frequency distribution for height



C.S. x C.S. (2 I That.) Monosomic B_{100} Lines

C.S. (2 I Tim.) x C.S. (2 I That.) Monosomic B_{100} Lines

C.S. (2 I Hope) x C.S. (2 I That.) Monosomic B_{100} Lines

Figure 4. Frequency distribution for height

Two main height classes are evident in each distribution. In every case the plants that were assigned EE and Ee genotypes for earliness fall in the short plant category and the plants of ee genotype fall in the tall plant category.

Since no individuals change classes with respect to the characters height and days to heading, it is almost certain that one gene with pleiotropic effects rather than two closely linked genes are responsible for the observed segregation for height and earliness.

The segregation of genes with minor effects on height will be considered later.

The Relationship between Height and Earliness

Each of the over-all means of the B_{100} lines derived from disomic B_{10} parent plants of each of the genotypes EE, Ee and ee is listed in Table 1 for the characters height and number of days to heading for each of the families C.S. x C.S. (2 I That.), C.S. (2 I Tim.) x C.S. (2 I That.) and C.S. (2 I Hope) x C.S. (2 I That.). In Figure 5 the over-all means for height of the three genotypic classes are plotted against the corresponding means for the character days to heading for each family. Included in the figure are coordinates designated as ee* which correspond to the mean height vs. the mean number of days to heading of lines of ee genotype grown from seed harvested in the fall of 1959.

It appears that there exists a functional relationship between height and number of days to heading, as is indicated by the results when presented graphically (Figure 5).

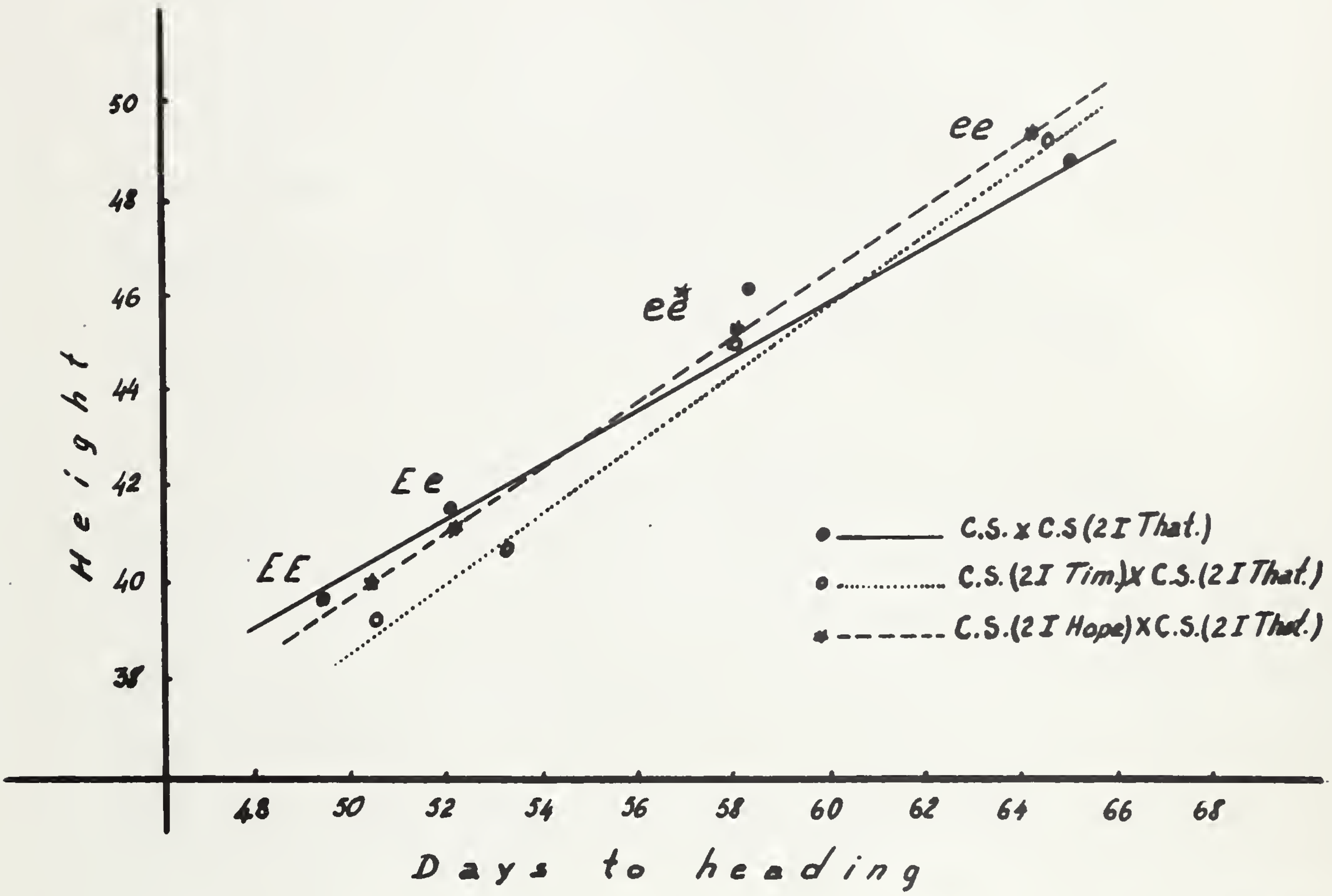


Figure 5. The relationship between height and number of days to heading

The Effect of the Gene (E) on the Characters Studied

In the terminology of Mather (1949) the deviation of the ee phenotype from the mid-parental value of $\frac{1}{2}$ (Value EE + Value ee) will be denoted as d, the deviation of the EE phenotype from the mid-parental value will be denoted as - d, and the deviation of the Ee phenotype from the mid-parental value will be denoted as h. In this experiment an estimate of h was obtained for the characters weight per plant and number of tillers per plant from the means of B_{100} lines from B_{10} parents of Ee genotype which contain EE, Ee and ee plants in a ratio of 1 : 2 : 1 and, therefore, deviate from the mid-parental value by $\frac{1}{4}d + \frac{1}{2}h - \frac{1}{4}d = \frac{1}{2}h$.

However, in the analysis of variance of the characters height and number of days to heading, the median value of the character measured in each row was used rather than the arithmetic average value. Since the gene (E) is partially dominant the plant with the median value in the progeny of a plant of genotype Ee should usually be of genotype Ee, and the difference between the over-all mean of these lines and the mid-parental value should provide a valid estimate of h.

The values of d and h as well as the over-all mean values for the B_{100} lines derived from disomic B_{10} parents of each of the genotypes EE, Ee and ee is listed in Table 1 for the characters days to heading, height, total weight per plant, and number of tillers per plant. The standard errors (S.E.) that are given were calculated by using the formula:

$$\text{S.E. (EE)} = \pm \left(\frac{V_{EE}}{N_{EE}} \right)^{\frac{1}{2}}, \quad \text{S.E. (Ee)} = \pm \left(\frac{V_{Ee}}{N_{Ee}} \right)^{\frac{1}{2}}, \quad \text{S.E. (ee)} = \pm \left(\frac{V_{ee}}{N_{ee}} \right)^{\frac{1}{2}},$$

$$\text{S.E. (d)} = \pm \tfrac{1}{2} \left(\frac{V_{EE}}{N_{EE}} + \frac{V_{ee}}{N_{ee}} \right)^{\frac{1}{2}}, \text{ and S.E. (h)} = \pm \left(4 \frac{V_{Ee}}{N_{Ee}} + \frac{V_{EE}}{N_{EE}} + \frac{V_{ee}}{N_{ee}} \right)^{\frac{1}{2}}.$$

In the case of height and number of days to heading the last formula was replaced by

$$\text{S.E. (h)} = \pm \left(\frac{V_{Ee}}{N_{Ee}} + \tfrac{1}{4} \frac{V_{EE}}{N_{EE}} + \tfrac{1}{4} \frac{V_{ee}}{N_{ee}} \right)^{\frac{1}{2}}.$$

V_{ee} and V_{Ee} were calculated from the observed variance of B_{100} lines within the ee and Ee genotypic classes respectively, and V_{EE} was calculated directly from the mean error variance obtained from the analysis of variance. N_{Ee}, N_{EE} and N_{ee} are the numbers of B_{100} lines in the Ee, EE and ee classes respectively.

The given standard errors together with the number of lines in each class shown in Figures 1 and 2 suffice for the calculation of tests of significance.

Detection of Modifying Genes

Within the EE, Ee and ee genotypic classes a "residual variance" (V_R) can be calculated. Because few EE lines are present in each experiment, the "residual variance" is calculated only from the variance of the disomic B_{100} lines within the Ee and ee classes and is equal to

$$V_R = \frac{V_{Ee} + V_{ee}}{N_{Ee} + N_{ee} - 2}.$$

Table 1. Means of B_{100} lines from discmic parents of genotypes EE, Ee and ee, and the corresponding values of d and h

Character	Family	Genotype of B_{10} Parent				
		EE	Ee	ee	d	h
Number of days to heading	C.S. x C.S. (2 I That.)	49.45 ± 0.39	52.06 ± 0.24	65.18 ± 0.36	7.86 ± 0.27	-5.26 ± 0.36
	C.S. (2 I Tim.) x C.S. (2 I That.)	50.50 ± 0.74	53.20 ± 0.32	64.71 ± 0.21	7.10 ± 0.38	-4.40 ± 0.51
	C.S. (2 I Hope) x C.S. (2 I That.)	50.38 ± 0.47	52.10 ± 0.42	64.50 ± 0.36	7.06 ± 0.29	-5.34 ± 0.51
	Average				7.34 ± 0.18	-5.00 ± 0.27
Height (inches)	C.S. x C.S. (2 I That.)	39.80 ± 0.57	41.73 ± 0.43	48.94 ± 0.34	4.57 ± 0.33	-2.65 ± 0.54
	C.S. (2 I Tim.) x C.S. (2 I That.)	39.20 ± 0.67	40.80 ± 0.30	49.48 ± 0.26	5.39 ± 0.36	-3.79 ± 0.47
	C.S. (2 I Hope) x C.S. (2 I That.)	40.00 ± 0.58	41.26 ± 0.52	49.47 ± 0.40	4.73 ± 0.35	-3.48 ± 0.63
	Average				4.90 ± 0.20	-3.31 ± 0.32
Total weight per plant (grams)	C.S. x C.S. (2 I That.)	36.12 ± 2.04	39.99 ± 1.67	47.53 ± 1.36	5.70 ± 1.23	-3.68 ± 4.15
	C.S. (2 I Tim.) x C.S. (2 I That.)	30.00 ± 3.47	39.34 ± 1.55	47.46 ± 0.93	8.73 ± 1.80	-1.21 ± 4.74
	C.S. (2 I Hope) x C.S. (2 I That.)	40.15 ± 1.92	41.13 ± 1.72	49.50 ± 0.93	4.68 ± 1.07	-7.40 ± 4.40
	Average				6.37 ± 0.81	-4.10 ± 2.50
Number of tillers per plant	C.S. x C.S. (2 I That.)	12.45 ± 0.50	12.93 ± 0.39	15.01 ± 0.32	1.28 ± 0.30	-1.60 ± 0.98
	C.S. (2 I Tim.) x C.S. (2 I That.)	10.30 ± 0.74	12.77 ± 0.34	14.43 ± 0.20	2.06 ± 0.39	-0.80 ± 1.02
	C.S. (2 I Hope) x C.S. (2 I That.)	12.74 ± 0.53	12.60 ± 0.48	14.27 ± 0.27	0.77 ± 0.30	-1.82 ± 1.13
	Average				1.37 ± 0.19	-1.41 ± 0.69

Under the null hypothesis that V_R is due only to environmental variation, V_R should be equal to the estimate of the mean error variance (V_{error}) of B_{100} line means calculated with N degrees of freedom from the analysis of variance. Following Kenney and Keeping (1951) $F = V_R / V_{error}$ with $N_{Ee} + N_{ee} - 2$ and N degrees of freedom provides an appropriate test of the null hypothesis.

Any real difference between V_R and V_{error} is probably due to the segregation of genes with small effects. The "residual genetic" variance may then be denoted by $V_G = V_R - V_{error}$.

On the hypothesis that all of the "residual genetic" variance is due to the segregation of genes on chromosome I, the variance (V_W) between the B_{100} lines derived from the same B_1 ancestor should equal the environmental error variance (V_{error}). Again following Kenney and Keeping (1951) a test of the significance of the hypothesis is provided by $F = V_W / V_{error}$.

In Table 2 the "residual genetic" variances are tabulated for the characters studied in each family. Whenever the significance of a V_G entry is probably largely due to the segregation of genes on chromosomes other than chromosome I, as indicated by a significant $F = V_W / V_{error}$, the V_G entry is followed by the letters b.g. However, because of the scarcity of duplicate B_{100} lines from the same B_1 ancestor, the test for segregation of genes on "background chromosomes" could not be applied effectively in several families, including the C.S. x C.S. (2 I That.) family.

Table 2. "Residual genetic" variances

Family	Days to Heading	Height	Number of Tillers per Plant	Weight per Plant
C.S. x C.S. (2 I That.)	2.31^{**}	1.17^{*}	1.04^{*}	20.9^{*}
C.S. x C.S. (2 I Tim.)	$2.89^{**}_{b.g.}$	0.57	0.98^{*}	5.57
C.S. x C.S. (2 I Hope)	$2.10^{**}_{b.g.}$	0	0.918^{*}	$27.16^{*}_{b.g.}$
C.S. (2 I Tim.) x C.S. (2 I That.)	0.05	0.28	0.01	0
C.S. (2 I Tim.) x C.S. (2 I Hope)	1.67	1.14	0.65	0
C.S. (2 I Hope) x C.S. (2 I That.)	0.995^{**}	1.18^{*}	0	3.2

* Significant at the 95% level

** Significant at the 99% level

b.g. F value indicating segregation of genes on "background" chromosomes is significant at the 95% level

DISCUSSION

It was found that the characters height, days to heading, weight per plant, and number of tillers per plant were markedly affected by one gene or by several closely linked genes. The effects of the gene (genes) on days to heading and height were particularly striking. Because no obvious crossovers were observed in any of the 134 B_{100} lines studied, it is probable that only one gene, designated E, with pleiotropic effects was responsible for the observed segregation for height and number of days to heading. If two genes, one affecting mainly earliness and the other affecting mainly height, were involved in the inheritance of height and earliness, it would seem logical to suppose that one gene could have any degree and direction of dominance independent of the degree and the direction of dominance of the other gene. It is found, however, that the degree of dominance is about $h/d = -0.68$ for number of days to heading, $h/d = -0.68$ for height, and $h/d = -0.64$ for total weight per plant. This would indeed be a strange coincidence if two or three closely linked genes were responsible for the observed effects, but would be expected if almost linear functional relationships existed between the characters. Any such functional relationships would undoubtedly have a physiological or biochemical basis.

It is found that ee^* lines, which are genotypically the same as ee lines but are grown from seed harvested in the field rather than in the greenhouse, are earlier than ee lines. The physiological reason

for the comparative earliness of the ee* lines is unknown, but if earliness *per se* influences height, then the same functional relationship between height and number of days to heading that was found before should hold. That this is indeed the case is illustrated in Figure 5 where the ee* coordinates fall very near the straight lines that approximate the postulated functional relationship.

It may be concluded, therefore, that not only can an individual "polygene" (in Mather's terminology) be proven to have pleiotropic effects, but also that pleiotropic effects may be expected on physiological grounds.

Appraisal of the Value of this Technique to Study the Genetics of Characters with Quantitative Expression

One criterion of the value of a technique is that few untestable assumptions need be made in the application of the technique. If the genetics of chromosome I of wheat had been studied in the substitution lines used in this investigation by means of orthodox breeding procedures, a rather natural assumption might have been that the gene found to have the greatest effects on the characters studied was located on chromosome I. That the assumption would have been incorrect is clearly demonstrated in this investigation in which were employed monosomic breeding procedures that make possible two effective tests of whether or not a gene is on a substituted chromosome.

The use of the technique does not appear to be restricted to the study of genes with rather large phenotypic effects. It was found that relatively small "residual genetic" variances could be shown to be statistically significant (see Table 2). Furthermore, it could be

shown that the significance of several of these were largely due to genes which were not on chromosome I.

The experimental technique, therefore, shows promise of being capable of detecting the effects of individual genes with very small effects. The sensitivity of the method used could, however, be greatly increased, especially for the study of very variable characters such as yield, by increasing the number of lines field tested, the number of plants per plot and the plot size, and the number of replicates used.

One important aspect so clearly evident from these studies is that a total of at least 7 to 8 backcrosses should be made in the production of substitution lines. Also, care should be exercised in the use of female monosomic plants of the recurrent parent in such a way that no plants which have a selective advantage due to a gene or genes on chromosomes other than the substituted one are unconsciously automatically selected. If the above considerations are kept in mind, reconstitution of the recipient parent except for the substituted chromosome will be complete enough to permit a more critical and precise analysis of the gene content of the substituted chromosome.

The Possible Location of the Gene, E, and Some Considerations on the Quantitative Genetic Differences between Chinese and Thatcher Wheats

Because the gene, designated E, was not located on chromosome I of Thatcher, it should be present in one or more of the remaining substitution lines in the "Thatcher set" of substitution lines studied by Kuspira and Unrau (1957). The phenotypic expression of

these lines should be similar to that of C.S. (2 I That.) and therefore it may be possible to determine which substitution line carries the gene (E) on its substituted chromosome.

According to Kuspira and Unrau (Personal Communication) three backcrosses to Chinese monosomics had been made before field testing of the substitution lines was begun. The probability then that a particular gene on a "background" chromosome will be present in a substitution line is $(1/2)^3 = 1/8$. The expected number of substitution lines having the gene on a background chromosome is $1/8 \times 20 = 2.5$ with a standard error of about 1.48*. Unfortunately only 19 substitution lines were available in the "Thatcher set" of substitution lines used in the study by Kuspira and Unrau (1957). Therefore, the above consideration is not valid. However, if the assumption is made that a particular gene is on a substituted chromosome in one of the 19 substitution lines in the set studied by Kuspira and Unrau, then the expected number of substitution lines having a particular gene on a "background chromosome" is $1/8 \times 18 = 2.25$ with a standard error of about 1.4. Therefore, $1 + 2.25 = 3.25$ of the substitution lines in the set are expected to carry the gene.

If an allele derived from Thatcher is on a "background chromosome" of a substitution line and has a selective advantage over the allele found in Chinese, it should after a few generations (as during seed multiplication) be present in high frequency, and its effects might readily be detected in field trials. In any case one substituted

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* Following rules of statistics (see, for example, Kenney and Keeping, 1951.)

chromosome will carry the gene in homozygous condition and, therefore, at least one substitution line should show the phenotypic effects of the gene.

Kuspira and Unrau (1957) present data on the number of days to head of the "Thatcher set" of substitution lines. On the basis of their data a graph of the distribution for number of days to head of the substitution lines in the set was constructed and is presented in Figure 6.

Five apparently distinct groups with from two to five substitution lines in each are evident in the distribution. The number of lines in each group agrees well with the number expected (1.85 to 4.65) if the lines in each group, other than the one containing Chinese (C.S.), carried a gene differentiating them from Chinese for earliness. Therefore, it is likely that four main genes (or closely linked groups of genes) are responsible for differentiating Chinese from Thatcher for earliness.

The gene (E) of most interest in this investigation is found in C.S. (2 I That.) which is in the earliest group. It may, therefore, be expected that the gene is on one of chromosomes III, VI, VIII, or XII whose substitution lines are also in the earliest group.

From the results of this investigation, it might be expected that an individual gene might affect several different characters. For example, a scrutiny of the data presented by Kuspira and Unrau (1957) revealed that all of the substitution lines in the earliest class were found to have a relatively low protein content of 14.1 to

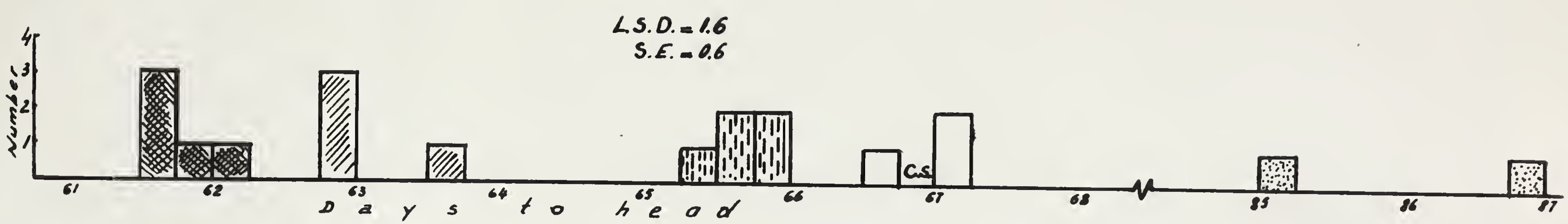

Figure 6. Frequency distribution for days to head of Thatcher set of substitution lines
(Based on data given by Kuspira and Unrau, 1957)

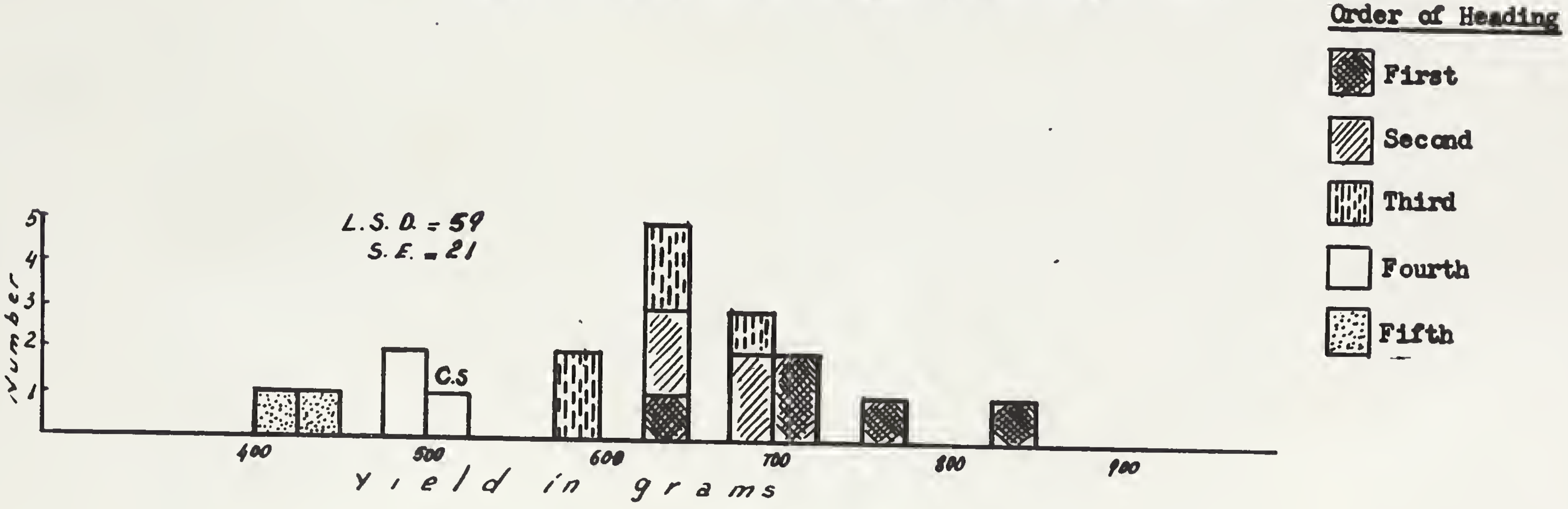

Figure 7. Frequency distribution of yield in grams of Thatcher set of substitution lines
(Based on data given by Kuspira and Unrau, 1957)

14.4 per cent. The low protein content, however, did not appear to be due only to the earliness of the lines, because three of the five substitution lines found by Kuspira and Unrau (1957) to have highly significantly higher protein contents than Chinese were in the group which was second in the order of heading. Therefore, the gene responsible for the earliness of the group either also has an effect on protein content or is closely linked to a gene which has a marked effect on protein content.

It was also found that all of the substitution lines listed by Kuspira and Unrau (1957) as significantly higher yielding than Chinese were in the earliest group. In fact it is found that, in general, yield progressively decreased with order of heading. The distribution for yield of the "Thatcher set" of chromosomes is presented in Figure 7. Distinct groups or classes are not evident in the distribution for yield, and the genetic complexity of yield inheritance cannot be ascertained from a knowledge of the distribution alone. However, it is likely that the four genes conditioning earliness that were found, do contribute to the observed variation in yield.

It was calculated from the data presented by Kuspira and Unrau (1957) that the total variance (V_T) of the means of the "Thatcher set" of substitution lines for yield was $V_T = 12,106.12$ (d.f. = 18) and that the variance (V_W) of means within heading order classes was $V_W = 2,296.01$ (d.f. = 14). From data presented in a thesis by Kuspira (1955) it was calculated that the error variance (V_E) of means was $V_E = 434.77$ (d.f. = 240). An estimate of the genetic variance (V_G) of

the substitution lines is then

$$V_G = V_T - V_E = 12,106.12 - 434.77 = 11,671.35.$$

An estimate of the variance (V_R) due to genes other than the four genes conditioning earliness and genes closely linked to them is

$$V_R = V_W - V_E = 2,296.01 - 434.77 = 1,861.24.$$

An estimate of the variance (V_{Earl}) due to the four genes conditioning earliness and genes closely linked to them is then

$$V_{Earl} = V_G - V_R = 9,810.11.$$

Therefore, approximately 85 per cent of the genetic variance of the substitution lines for the character yield may have been due to four genes which primarily affect earliness.

Although far too few lines were available for a comprehensive analysis of the genetic differences between Chinese and Thatcher, substantial evidence is presented to support the view that far fewer genes are responsible for most of the genetic variation in even such complex characters as yield than is usually postulated.

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